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Pseudalopex culpaeus.

By Andrés J. Novaro

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Pseudalopex Burmeister, 1856

Pseudalopex Burmeister, 1856:24. Type species *Canis magellanicus* Gray, 1837*a* (a subspecies of *P. culpaeus*), by subsequent designation.

Pseudolycos Philippi, 1903:157. No species mentioned.

Cerdocyon Allen, 1905:154 (not *Cerdocyon* Hamilton Smith, 1839).

Angusticeps Hilzheimer, 1906:114. Type species *Canis* (*Angusticeps*) *reisii* Hilzheimer, 1906 (a subspecies of *P. culpaeus*), by subsequent designation.

Microcyon Trouessart, 1906:1186. Type species *Speothos riveti* Trouessart, 1906 (a synonym of *P. c. reissii*), by subsequent designation.

Dusicyon Kraglievich, 1930:57 (part, not of Hamilton Smith, 1839).

CONTEXT AND CONTENT. Order Carnivora, Family Canidae, Subfamily Caninae. The genus *Pseudalopex* includes five or six species (Berta, 1987; Tedford et al., 1995; Wozencraft, 1993; Yahnke et al., 1996; Zunino et al., 1995): *P. culpaeus*; *P. peruanus* (extinct); *P. griseus*; *P. gymnocercus*; *P. fulvipes*; *P. sechurae*. Zunino et al. (1995) studied cranial measurements and pelage characters of *P. gymnocercus* and *P. griseus* and concluded that they are conspecific. A key to living species of *Pseudalopex* (modified from Cabrera, 1932; Clutton-Brock et al., 1976; Crespo and De Carlo, 1963; Eisenberg, in press; Ginsberg and Macdonald, 1990; Osgood, 1943; Redford and Eisenberg, 1992) follows:

1. Tail not bushy and <50% of length of head and body; uniformly dark and rufous pelage; size small, length of head and body 490-542 mm ..... *P. fulvipes*
   Tail bushy and >50% of length of head and body; size small to medium, length of head and body 446–1010 mm 2
2. Short, coarse fur; overall pale coloration, little or no rufous coloring on the body; size small, length of head and body 530–590 mm; skull without an interparietal crest ..... *P. sechurae*
   Fur neither short nor coarse; coloration not pale; small to medium size, length of head and body 446–1010; skull with or without interparietal crest. 3
3. Whitish chin; brownish patch of pelage on back of thighs; skull with interparietal crest; medium size, length of head and body 585–1010 mm ..... *P. culpaeus*
   Black chin; black patch of pelage on back of thighs; skull with or without interparietal crest; size small, length of head and body 446–722 mm 4
4. Length of cranium and hind foot ca. 150 mm; length of head and body 520–722 mm; color of pelage relatively uniform ..... *P. gymnocercus*
   Length of cranium <135 mm and length of hind foot <130 mm; length of head and body 446–660 mm; feet tawny and head rust colored ..... *P. griseus*

Pseudalopex culpaeus (Molina, 1782)

Culpeo Fox

Canis culpaeus Molina, 1782:293. Type locality "Chili." Cabrera (1931) suggested that it was restricted to "Santiago Province," Chile, now called Chilean Region V.

Vúlpes magellánica Gray, 1837*b*:578. Type locality "Magellan's Straits" (=Port Famine; Gray 1843:61), Magallanes, Chile.

Canis (*Pseudalopex*) *lycoides* Philippi 1896:542. Type locality "insulis Tierra del Fuego," Magallanes, Chile.

Canis amblyodon Philippi, 1903:158. Type locality "provincia Valparaíso," Chile.

Canis albigula Philippi, 1903:159. Type locality "provinciis centralibus," Chile.

Canis (*Cerdocyon*) *prichardi* Trouessart, 1904:234. New name for *Canis montanus* Prichard, 1902:260 (preoccupied); type locality "South-eastern Patagonia."

Canis (*Angusticeps*) *reissii* Hilzheimer, 1906:116. Type locality "Quito," Pichincha, Ecuador. Cabrera (1958) suggested Volcán Cotopaxi, Pichincha Province, Ecuador.

Speothos riveti Trouessart, 1906:1185. Type locality "Alchipichi, province de Pichincha (Equateur), altitude de 2101m," Ecuador.

Pseudalopex culpaeus Thomas, 1914*a*:357. First use of current name.

Pseudalopex culpaeolus Thomas, 1914*a*:359. Type locality "Santa Elena," Soriano, Uruguay. Considered a composite (skin of *P. culpaeus*; skull of *P. gymnocercus*) by Langguth (1967) who selected the skin as lectotype.

Pseudalopex inca Thomas, 1914*a*:361. Type locality "Sumbay, Arequipa, Peru. Alt. 4000 m." Considered a composite (skin of *P. gymnocercus*; skull of *P. culpaeus*) by Langguth (1967) who selected the skull as lectotype.

Pseudalopex smithersi Thomas, 1914*b*:573. Type locality "Sierra de Cordoba," Córdoba, Argentina. Cabrera (1958) suggested Pampa de Achala (2200 m).

Canis ferrugineus Huber, 1925:9. Type locality "la Cordillera (de los Andes), entre los ríos Mendoza, Atuel, Neuquén y Collón-Curá," Argentina.

CONTEXT AND CONTENT. Context noted in generic account. Six subspecies are recognized as follows (Cabrera, 1931):

P. c. andina Thomas, 1914*a*:357. *P. culpaeolus* Thomas and *P. inca* Thomas are synonyms. Type locality "Esperanza, near Mt. Sajama, Province of Oruro (La Paz), Bolivia. Alt. 4000 m."

P. c. culpaeus (Molina, 1782). See above. *C. amblyodon* Philippi, *C. albigula* Philippi, and *C. ferrugineus* Huber are synonyms.

P. c. lycoides (Philippi, 1896). See above.

P. c. magellanica (Gray, 1837*a*). See above. *C. prichardi* Trouessart is a synonym.

FIG. 1. Adult male and female *Pseudalopex culpaeus* from Monumento Natural Bosques Petrificados, Santa Cruz Province, Argentina. Photograph by P. Colavino.

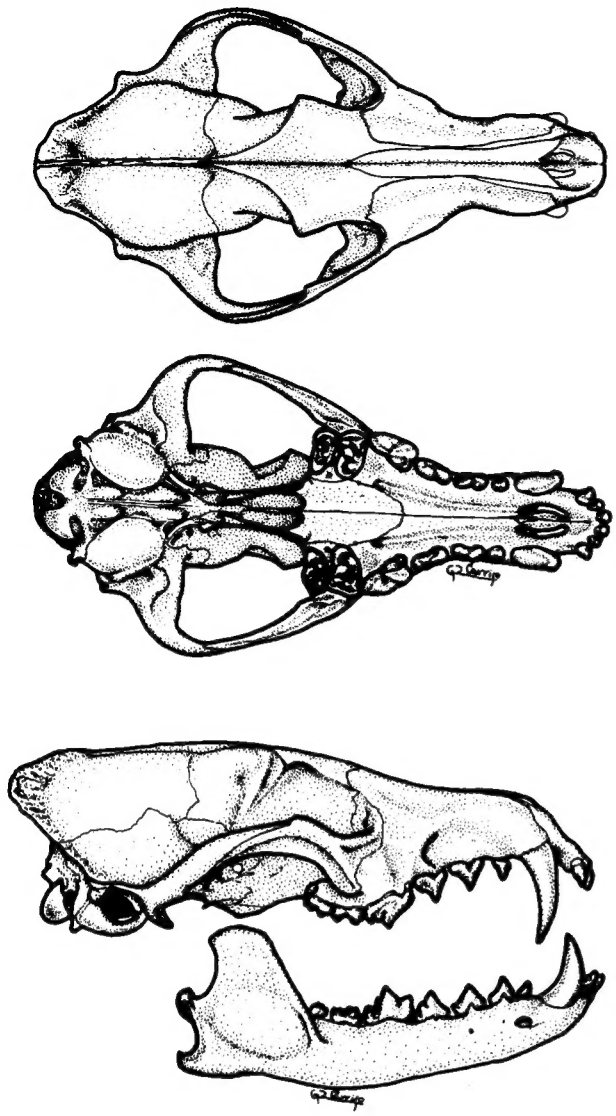

FIG. 2. Dorsal, ventral, and lateral view of cranium and lateral view of mandible of *Pseudalopex culpaeus* from Catán Lil, Neuquén Province, Argentina (female, Museo Argentino de Ciencias Naturales specimen 15056). Greatest length of cranium is 174 mm. Drawn by G. Carrizo.

P. c. reissii (Hilzheimer, 1906). See above. *S. riveti* Trouessart is a synonym.

P. c. smithersi Thomas, 1914*b*. See above. Langguth (1969) lists this subspecies as a synonym of *P. c. andina*.

DIAGNOSIS. *Pseudalopex culpaeus* is distinguished from congenerics by its larger size (length of head and body, 585–1010 mm, 446–722 mm, respectively), narrower rostrum (rostrum width 24% of palate length in culpeos, 27–32% in other species), reddish coloration of the head, neck, ears, and legs, and white to light-tawny chin (Cabrera and Yepes, 1940; Clutton-Brock et al., 1976; Crespo and De Carlo, 1963; Eisenberg, in press; Osgood, 1943; Redford and Eisenberg, 1992). Furthermore, the tail of *P. fulvipes* is not bushy and is shorter relative to the length of head and body; pelage color of *P. gymnocercus* is more uniform; *P. griseus* and *P. sechurae* lack the interparietal crest; and in the latter there is little or no rufous coloring on the body, and the palatine bones extend backwards beyond the posterior edge of M2 (Clutton-Brock et al., 1976).

GENERAL CHARACTERS. *Pseudalopex culpaeus* (Fig. 1) is a large fox. Its skull has a long and narrow facial region, flat frontal bones, a slightly developed interparietal crest, and a continuous sagittal crest (Fig. 2). The palatine bones do not extend backwards beyond the posterior edge of M2. Canines and premolars are simple and "fox-like" and the metaconid of m1 is higher than the level of the talonid (Clutton-Brock et al., 1976; Langguth, 1969). *P. culpaeus* has a reduced m2 metaconid (Berta, 1987).

The dorsal part of the head, neck, outer aspect of the ears and legs, and flank regions of *P. culpaeus* are tawny or rufous. The back and shoulders are gray with agouti (banded black and white) guard hairs, underparts are pale, and underfur is fawn. Black hairs predominate along the center of the back, forming a distinctive dark line that varies in width among subspecies. The dorsal sides of the feet are light tawny. *P. culpaeus* has a bushy tail that is >50% of the length of head and body, is black-tipped, and has a black spot on the upper side near the base (Clutton-Brock et al., 1976; Langguth, 1969).

Pseudalopex culpaeus increases significantly in body size with increasing latitude in the southern portion of its range (Fuentes and Jaksic, 1979; Jiménez et al., 1995). In north-central Chile (Aucó, 31°30′S) adult mean body mass (in kg), length of body (in mm), and total length (in mm; n = 9) are 4.32, 628, and 999, respectively. The same measurements in southern Chile (Torres del Paine, 51°03′S; n = 7) are 10.16, 739, and 1,152, respectively. Mean body mass (in kg) at another site in northern-central Chile (Fray Jorge, 30°38′) is 6.52 (n = 5—Jaksic et al., 1993), and to the south in Neuquén Province, Argentina (39°33′S) it is 9.93 (n = 22—Novaro, 1991).

Adult male culpeos weigh significantly more than females in Torres del Paine (mean of 11.65 kg, n = 4, compared to 7.82 kg, n = 3—Johnson and Franklin, 1994*c*) and in Neuquén (11.02 kg, n = 11, compared to 8.84 kg, n = 11—Novaro, 1991). Mean external measurements (in mm; range and n in parentheses) for male and female culpeos, respectively, from Neuquén Province, are: total length, 1,150 (820-1,520; n = 150), 1,102 (900-1,1240; n = 107); length of tail, 412 (300-510; n = 130), 395 (315-455; n = 108); length of hind foot, 163 (140-181; n = 143), 152 (130–160; n = 106); length of ear, 88 (80-95; n = 144), 84 (76-90; n = 104—Crespo and De Carlo, 1963). Mean cranial and tooth measurements (in mm; n in parentheses) for males and females, respectively, from Neuquén Province, are: length of cranium, 171.0 (n = 139), 163.0 (n = 105); basal length, 156.6 (n = 128), 149.4 (n = 102); palatal length, 85.0 (n = 129), 81.2 (n = 102); zygomatic width, 85.0 (n = 129), 81.9 (n = 100); interorbital width, 27.9 (n = 126), 27.0 (n = 101); mastoid width, 49.3 (n = 136), 46.8 (n = 102); braincase width, 49.9 (n = 131), 49.8 (n = 103); c1-m2 length, 73.7 (n = 134), 72.0 (n = 96); mandible length, 126.8 (n = 143), 121.7 (n = 103—Crespo and De Carlo, 1963).

Subspecies of *P. culpaeus* differ in skull length, especially in the muzzle, in a north-south gradient along the Andean Cordillera (Thomas, 1914*a*). The muzzle and skull of *P. c. culpaeus* are longer (condylobasal length, 148–174 mm) than in the northern subspecies, *P. c. reissii* and *P. c. andina* (condylobasal length ca. 155 mm; rostrum length ca. 70 mm), and somewhat shorter than in *P. c. magellanica* (condylobasal length, 155-175 mm). *P. c. lycoides*, in Tierra del Fuego, has the longest muzzle and skull of all subspecies (condylobasal length, 185-201 mm; length of rostrum 86-94 mm—Crespo and De Carlo, 1963; Kraglievich, 1930; Langguth, 1967, 1969).

P. c. culpaeus has a light tawny chin, grayish body and upper side of the tail, tawny head, bright tawny feet and legs, and dull tawny under-side of tail. Pelage of *P. c. andina* is similar, but is paler throughout (Osgood, 1943); the head, legs and feet are ochraceous tawny rather than tawny (Osgood, 1943). *P. c. andina* is similar to *P. c. reissii* in skull characters, but coloration of *P. c. andina* is more suffused with buff above, especially anteriorly, the heavy black grizzling starts further back, and pelage is whiter below (Thomas, 1914*a*). The two southernmost forms, *P. c. lycoides* and *P. c. magellanica*, also differ in that the former has an overall grayish coloration with gray throat and chest while the latter is more rufous with white throat and chest (Philippi, 1896). *P. c. lycoides* is the largest of all subspecies, frequently reaching a total length of 1,500 mm (Cabrera and Yepes, 1940). *P. c. smithersi* is characterized by its small size (condylobasal length of skull, 143–148 mm; length of rostrum ca. 65 mm) and an intense ferruginous coloration (Kraglievich, 1930; Thomas, 1914*b*).

DISTRIBUTION. The culpeo fox inhabits semidesert Andean plateau, mediterranean scrub and grassland, and woodland areas of western and southern South America (Fig. 3; Crespo, 1975; Osgood, 1943). Its range extends from northern Ecuador (and per-

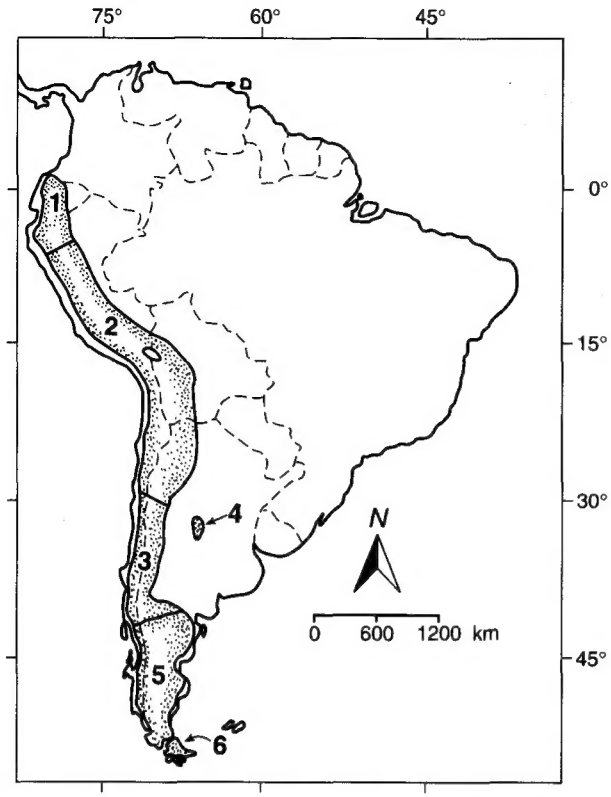

FIG. 3. Geographic distribution of *Pseudalopex culpaeus* in South America. Numbers correspond to approximate ranges (boundaries for subspecies 1, 2, 3, and 5 are not well established) of subspecies (Cabrera, 1931, 1958): 1, *P. c. reissii*; 2, *P. c. andina*; 3, *P. c. culpaeus*; 4, *P. c. smithersi*; 5, *P. c. magellanica*; 6, *P. c. lycoides*.

haps southern Colombia, Nariño Province—Jiménez et al., 1995) to southern Chile and Argentina, along the foothills of the Andes, including Tierra del Fuego, and throughout the Patagonian steppe of Argentina (Redford and Eisenberg, 1992). In Ecuador it is found in the Andean region, as far north as Cotopaxi in Pichincha Province (IUCN, 1988). In Peru, culpeos also range throughout the Andean region at least between 1,000 and 4,500 m and in the highlands to the south (Grimwood, 1969).

Culpeo distribution may have expanded eastward in Argentina during the last century. According to early accounts (Prichard, 1902) culpeos were found only along the Andean Cordillera and its foothills during the early 1900s, but currently their range extends to the coast of Patagonia south of 43°S (Fig. 3). The increase in culpeo range may be related to the introduction of European hare (*Lepus europaeus*) and sheep (*Ovis aries*) in the early 1900s (Crespo and De Carlo, 1963; Grigera and Rapoport, 1983). Culpeo distribution in Chile also may be determined in part by the distribution and density of introduced lagomorphs and may have changed significantly during the last century (Johnson, 1992).

Isolated culpeo populations occur in the Córdoba hills of central Argentina and on the island of Tierra del Fuego. The former (subspecies *P. c. smithersi*) is separated from the remaining populations by the extensive, low plains of La Rioja Province (Cabrera, 1931). *P. c. lycoides* in Tierra del Fuego is separated from mainland populations by the Straits of Magellan.

FOSSIL RECORD. South American canids originated in North and Central America and migrated south after emergence of the Panamanian Land Bridge ca. 3.0×10^6 years ago (Berta, 1981, 1988). Maximum diversification of canids occurred in South America, perhaps due to the absence of other carnivorous placental mammals and the presence of only a few species of carnivorous didelphids (Wayne and O'Brien, 1987; Webb, 1985). The earliest fossil records are *Pseudalopex* of the Chapadmalalan age ($3.0–1.8 \times 10^6$ years ago) in north and central Chile (Moreno et al., 1994) and *P. gymnocercus* (Fischer, 1814) of the Uquian age ($2.5–1.5 \times 10^6$ years ago; late Pliocene and early Pleistocene) in the Vorohué Formation, Buenos Aires Province, Argentina (Kraglievich, 1952; Pascual, 1966). Fossils of the genus *Pseudalopex* are also recorded from Ensenadan-age ($1.5–0.3 \times 10^6$ years ago; middle Pleistocene) deposits in Buenos Aires Province, Argentina, and in north and central Chile. The earliest record for *P. culpaeus* is from La Carolina, Ecuador, and corresponds to the Lujanian ($3.0–0.1 \times 10^5$ years ago; late Pleistocene—Berta, 1987; Moreno et al., 1994).

FORM AND FUNCTION. *Pseudalopex culpaeus* has a dental formula of i 3/3, c 1/1, p 4/4, m 2/3, total 42 (Berta, 1987). The molars in the larger subspecies of *P. culpaeus* are enlarged, but this is probably a consequence of larger body size rather than of specialization in food habits (Langguth, 1969). The culpeo fox, as in other species of the genus, has a long and coiled cecum (Langguth, 1969). The fur of *P. culpaeus* becomes longer and denser during the winter, particularly on the tail (Crespo and De Carlo, 1963). The front and hind feet have five and four toes, respectively, and the limb posture is digitigrade (Cabrera, 1932).

The increase in body size of culpeos in southern Chile may be the result of bioenergetic adaptation to colder regions (Jiménez et al., 1995). To meet daily energy requirements (calculated using theoretical basal metabolic rates), culpeo foxes need 0.4–1.2 European hares or 26–70 rodents in Chilean Patagonia. In north-central Chile, where culpeos are smaller, they need 0.2–0.4 lagomorphs or 3–6 rodents. These energy requirements have implications for culpeo distribution in relation to the distribution of introduced lagomorphs and medium-sized rodents such as *Octodon degus* and *Abrocoma bennetti* (Johnson, 1992).

ONTOGENY AND REPRODUCTION. Culpeo foxes in Neuquén Province, Argentina, have a period of sexual activity in both sexes from June through October (Crespo and De Carlo, 1963). They mate mainly between August and October and produce one litter per year, with a peak of births from October to December. Females are in anestrus from October to July, proestrus from the end of July to mid-October, and estrus from early August to October; estrus is followed by pregnancy or pseudopregnancy (males: $n = 51$; females: $n = 48$—Crespo and De Carlo, 1963). The gestation period is 55–60 days, and mean number of embryos is 5.2 ($n = 6$—Crespo and De Carlo, 1963). In Chile the gestation period is estimated at 65 days and litter size ranges from three to five young (Housse, 1953).

Young culpeos are born with their eyes closed. At 2 days of age a male weighed 166 g and a female 170 g (Crespo and De Carlo, 1963). Young culpeos are weaned at 2 months of age and grow to adult size within 7 months (Crespo and De Carlo, 1963). Both male and female may care for the young (Gittleman, 1986). By 1 year of age, developing males produce mature sperm in both testes, and females ovulate (Crespo and De Carlo, 1963).

ECOLOGY. *Pseudalopex culpaeus* lives in mountainous habitats, on the puna highlands up to 4,500 m, and on plains down to sea level on either side of the Andes mountain chain (Marquet et al., 1993; Medel and Jaksic, 1988). It occupies habitats that are either forested or covered by shrubby or herbaceous vegetation. In southern Chile and the Andean foothills of northwest Argentinean Patagonia, culpeos select *Nothofagus* thickets and matorral shrubland habitats where prey are more abundant and there is more cover for resting and den sites (Crespo and De Carlo, 1963; Johnson and Franklin, 1994*c*). In steppe habitat of northwest Patagonia, culpeos use humid valleys to forage and slopes and rugged areas to rest and den (Diuk Wasser, 1995).

Pseudalopex culpaeus is generally an opportunistic predator, although it can be locally selective for certain prey (Iriarte et al., 1989; Johnson and Franklin, 1994*a*; Meserve et al., 1987; Rau et al., 1987). Culpeos consume more vertebrate prey and less plant matter and invertebrates than any other South American canid (Redford and Eisenberg, 1992). Main prey items of culpeos are small mammals and introduced lagomorphs. Small mammals and European rabbits (*Oryctolagus cuniculus*) are consumed in varying proportions in central Chile (Ebensperger et al., 1991; Fuentes and Jaksic, 1979; Iriarte et al., 1989; Jaksic and Yañez, 1980; Jaksic et al., 1980; Yañez and Jaksic, 1978) and on Tierra del Fuego island (Jaksic and Yañez, 1983). European hares (*Lepus europaeus*) dominate the culpeo diet in the Magallanes Region of southern Chile (Johnson and Franklin, 1994*a*) and in northwest Argentinean Patagonia (Crespo and De Carlo, 1963; Novaro, 1991). Additional

prey include arthropods and fruit at most sites, mainly in Chile; sheep (*Ovis aries*, partly as carrion) in Argentinean Patagonia (Bellati and von Thungen, 1990; Crespo and De Carlo, 1963; Novaro, 1991) and Tierra del Fuego (Jaksic et al., 1983); birds (mainly *Chloephaga picta* and passerines) and guanacos (*Lama guanicoe*, probably as carrion) in southern Chile (Jaksic et al., 1983; Johnson and Franklin, 1994*a*; Yañez and Rau, 1980); and reptiles in central Chile (Ebensperger et al., 1991). In northern Chile culpeo foxes prey mostly on small rodents (Jaksic et al., 1993; Meserve et al., 1987), and to a lesser extent on reptiles, birds, arthropods, and fruit (Durán et al., 1987; Jaksic et al., 1992; Jiménez, 1993).

Functional and numerical responses of culpeo foxes to changes in prey availability vary among sites and type of prey. A functional response of prey switching (Jaksic and Simonetti, 1987) was recorded in central and southern Chile and Argentina. During seasons when availability of small mammals or hares declined, culpeos consumed increasing numbers of arthropods and fruit (Castro et al., 1994; Ebensperger et al., 1991; Jaksic et al., 1980; Johnson and Franklin, 1994*a*) or sheep (Crespo and De Carlo, 1963; Novaro, 1991). Culpeos did not display a functional response in their diet to marked changes in *Octodon degus* abundance, maintaining a strong preference for this species. However, culpeos displayed a significant numerical response following fluctuations in abundance of *O. degus* at Fray Jorge National Park in north-central Chile (Jaksic et al., 1993). Finally, culpeos did not show a functional or a numerical response during a decline of their rodent prey (mainly *O. degus* and *Abrocoma bennetti*) at Aucó in north-central Chile (Jaksic et al., 1992, 1996; Martínez et al., 1993).

Culpeo predation has significant effects on populations of small rodents that are overrepresented (relative to their availability) in the fox's diet (Meserve et al., 1996). Culpeo selectivity for rodent species has been related to the prey's habitat use and body size (Iriarte et al., 1989), body size and time of activity (Jaksic, 1986; Meserve et al., 1987), a combination of size and abundance (Jaksic, 1989; Jaksic et al., 1992), and higher vulnerability of certain cricetine species because of morphology (Corley et al., 1995).

Human disturbance may affect culpeo diets significantly. In areas of Chile and Argentina where sheep and European hare and rabbit were introduced, up to 96% of culpeo diet biomass is represented by these prey (Crespo and De Carlo, 1963; Johnson and Franklin, 1994*a*; Novaro, 1991; Simonetti, 1986). Habitat alteration by humans also may cause an increased consumption of *O. degus*, a rodent abundant in disturbed habitats (Simonetti, 1988). However, studies show that *O. degus* is the dominant item in culpeo diets even where this rodent is not the most abundant species (Iriarte et al., 1989; Meserve et al., 1987), suggesting that selectivity plays a more important role than human disturbance in determining culpeo food habits (Meserve, 1988).

The role of the culpeo fox as a disperser of tree seeds in central Chile is species-specific (Castro et al., 1994). Seeds of peumo (*Cryptocarya alba*) and pimiento (*Schinus molle*) defecated by culpeos are viable and germinate at higher rates than those not passed through digestive tracts, while seeds of litre (*Lithrea caustica*) germinate at lower rates. Seeds of pimiento are defecated in sites where successful establishment of seedlings is possible, whereas peumo seeds are not (Bustamante et al., 1992; Castro et al., 1994; León-Lobos and Kalin-Arroyo, 1994).

Culpeo population structure in Neuquén Province, Argentina was 77.5% for those 0–1 year of age, 13.8% for those 1-2 years of age, and 8.7% for those >2 years of age (Crespo and De Carlo, 1963). Sex ratio of the Neuquén population was significantly biased towards males in 1959-61 (1.45:1; $n = 254$—Crespo and De Carlo, 1963), but was not significantly different from a 1:1 ratio 30 years later (1.08:1; $n = 102$—Novaro, 1991). This change in sex ratio may be a response to increased hunting pressure (Novaro, 1995). Population density was 0.72 culpeos/km^2 in Neuquén Province (estimated by removal—Crespo and De Carlo, 1963) and 1.3 culpeos/km^2 in Torres del Paine National Park in Chile (estimated by strip census—Abello, 1979). Culpeo density in Neuquén increased after 1915 when European hares and sheep were introduced (Crespo and De Carlo, 1963), and it may be declining in Salta Province, Argentina (Mares et al., 1981).

The South American gray fox or chilla, *P. griseus*, may be a potential competitor of *P. culpaeus* (Fuentes and Jaksic, 1979; Jaksic et al., 1980, 1983). The two foxes are sympatric in many areas of Argentina and Chile, but appear to use different microhabitats. Culpeos use more wooded and densely vegetated habitats where their preferred prey are more abundant (Crespo and De Carlo, 1963; Jaksic et al., 1980; Jiménez, 1993; Jiménez et al., 1995). In southern Chilean Patagonia, culpeo and gray fox home ranges overlap little; they display a mosaic-type distribution, with culpeos occupying areas where European hares and rodents are more abundant. This pattern is likely dictated by the higher metabolic needs of culpeos and mediated by the aggressiveness of the larger culpeos and consequent avoidance by gray foxes (Johnson and Franklin, 1994*c*), although no direct culpeo-gray fox interactions have been recorded (Johnson and Franklin, 1994*b*). Other potential competitors of culpeos are lesser grisons (*Galictis cuja*), which prey on European rabbits, rodents, and reptiles (Ebensperger et al., 1991), Geoffroy's cat (*Oncifelis geoffroyi*) and pampas cat (*O. colocolo*), which prey on small mammals and birds (Johnson et al., 1992), and owls (*Speotyto cunicularia*, *Tyto alba*, *Bubo virginianus*, and *Glaucidium nanum*) and falconiforms (*Geranoaetus melanoleucus*, *Buteo polyosoma*, *Parabuteo unicinctus*, and *Falco sparverius*), which prey mainly on small mammals or lagomorphs (Jaksic et al., 1981, 1992, 1993; Meserve et al., 1987).

Parasite burdens in the digestive tracts of *P. culpaeus* from Neuquén, Argentina, are low. From one to five nematodes representing three species (*Physaloptera clausa*, *Toxascaris leonina*, and *Protospirura numidica criceticola*) were found in 5 of 129 culpeos studied. Arthropods and rodents are the main intermediate hosts; therefore, reduced predation by culpeos on these prey may explain the low prevalence of nematodes in Neuquén (Stein et al., 1994). The adult pentastomid *Linguatula serrata* was found in the trachea of culpeos from Chile. The larvae of this parasite are found in rodents and lagomorphs (Alvarez, 1960). Fleas (*Pulex irritans*) and biting lice (*Trichodectes canis*) are ectoparasites of culpeos (Crespo and De Carlo, 1963; Hopkins, 1949).

Prevalence of epidemiologically significant *Echinococcus granulosus* in culpeos from Neuquén was 12% in 1960 (6 of 50 culpeos—Szidat, 1960, 1963), 26% in 1971–1972 (9 of 34—Schantz et al., 1975), and 0% in 1989–1990 (0 of 129—Stein et al., 1994). The decline in the prevalence of *E. granulosus* in culpeos followed an intense campaign in Neuquén Province to treat domestic dogs against this cestode (C. Rambeaud, pers. comm.). Culpeos can become infected by eating infected sheep (Schantz et al., 1976), but larvae of *E. granulosus* are also found in European hares from Neuquén, which suggests the existence of a cycle with sylvatic hosts (Schantz et al., 1972). However, the low *E. granulosus* burdens in culpeos from Neuquén and the absence of infection in Chile (Alvarez, 1961; Blood and Lelijveld, 1969) suggest that culpeos are of limited importance in the transmission of this parasite (Schantz et al., 1975).

Inhabitants of the Andean region of Ecuador and Perú practiced hunts and burials of culpeo and Sechura-desert foxes for ceremonial purposes prior to 1750 B.C. (Wing, 1989). Culpeo foxes may have been domesticated by Indians on Tierra del Fuego (Hamilton Smith, 1839). Currently culpeos are intensively hunted in Argentinean Patagonia, both for their fur and to reduce predation on sheep and goats (Bellati and von Thungen, 1990; Ginsberg and Macdonald, 1990). Culpeos kill up to 7% of lambs born each year in northwest Patagonia (Bellati, 1986). Commercial hunting of culpeos is done mainly by rural workers, who supplement their incomes with sales of fox fur (Novaro, 1993). Simulations of culpeo population dynamics indicate that the current harvest in Argentinean Patagonia may be sustainable because of heterogeneous distribution of hunting, which is a consequence of topography and different levels of hunting pressure on sheep and cattle ranches (Novaro, 1995). This conclusion is supported by the results of monitoring programs of culpeo density throughout southern Argentina (Novaro and Funes, 1994; von Thungen, 1991), except in Tierra del Fuego (N. Loekemeyer, pers. comm.). Culpeo hunting was banned in Chile in 1980 (Iriarte and Jaksic, 1986), but illegal hunting is common outside protected areas (Jiménez, 1993). The species is included in Appendix II of CITES (Medel and Jaksic, 1988).

Researchers studying food habits of culpeos in areas of sympatry with other carnivores may encounter difficulties identifying their feces (Jiménez, 1993; Johnson and Franklin, 1994*a*). Jiménez et al. (1996) attempted to differentiate feces of culpeo and chilla foxes using thin-layer chromatography of their bile acid contents, but were not able to consistently profile bile acid standards. Capurro et al. (in press) successfully distinguished feces of culpeos and chillas with an improved bile-acid thin-layer chromatography

technique and reported bile-acid profiles of six other Neotropical carnivores potentially sympatric with culpeos.

BEHAVIOR. *Pseudalopex culpaeus* is primarily nocturnal in southern Chile and northwest Argentinean Patagonia, where it was studied with radio-telemetry (Diuk Wasser, 1995; Johnson and Franklin, 1994*c*). Culpeo activity in southern Chile increases dramatically within an hour or two of sunset and decreases near sunrise. In central Chile culpeos are either crepuscular (Jaksic et al., 1980) or active during day and night (Iriarte et al., 1989), although these conclusions are inferred from the activity patterns of the prey of *P. culpaeus*.

Surplus killing of lambs by culpeos is reported in Rio Negro Province, Argentina. Culpeos did not feed on 48% of their kills (n = 157—Bellati and von Thungen, 1990).

Annual and seasonal home range sizes of culpeos in southern Chile averaged 9.8 km^2 and 7.7 km^2 (n = 8), respectively. There were no significant differences in home range sizes among seasons and between sexes (Johnson and Franklin, 1994*c*).

Culpeo vocalizations in the field have not been described (Branch, 1994). Captive culpeos make a mixed growl/scream sound (Cohen and Fox, 1976).

GENETICS. The culpeo fox has a diploid number of 74, a fundamental number of 76, and all telocentric autosomes (Vitullo and Zuleta, 1992). The karyotype is identical to other species of the genus (Tedford et al., 1995). *P. culpaeus* and *P. griseus* have the southernmost range of species in South America and are likely to represent the most recent speciation events in the radiation of *Pseudalopex* species (Wayne et al., 1989; Yahnke et al., 1996). Based on polymorphisms in mitocondrial DNA restriction sites, the two species diverged approximately 2.5–5.0 × 10^5 years ago, and have evolved substantial differences in body mass and dental and cranial morphology over this relatively short time span. Character divergence may have been fostered by low prey and predator diversity present in South America when the species evolved during the Plio-Pleistocene (Wayne et al., 1989).

The Samson mutation is characterized by the absence of guard hairs and a yellowish-white appearance of fur caused by the underhair coloration (Voipio, 1950). This mutation is present in 3.5% of the population (9 of 257 culpeos) in northwestern Patagonia, Argentina (Crespo and De Carlo, 1963).

REMARKS. The taxonomic status of the genus of culpeo fox is unresolved. Cabrera (1931, 1940) gave *Pseudalopex* Burmeister, 1856 the rank of genus, included the culpeo fox in it, and considered it separate from *Lycalopex* Burmeister, 1854. Osgood (1934) found insufficient evidence to support generic separation of *Pseudalopex* from the genus *Dusicyon*. In a later study, Cabrera (1958) accepted the inclusion of the genus *Pseudalopex* into the genus *Dusicyon*. Langguth (1969, 1970) considered *Pseudalopex* a subgenus of *Dusicyon*. Ewer (1973) also assigned the group to the genus *Dusicyon*, whereas Langguth (1975) and Van Gelder (1978) gave *Pseudalopex* the rank of subgenus of the genus *Canis*. In a numerical classification of the family Canidae, Clutton-Brock et al. (1976) suggested placing the culpeo fox in the genus *Dusicyon*, and even doubted the recognition of different species previously assigned to *P. culpaeus* and *P. gymnocercus*. Based on a cladistic analysis of South American canids, Berta (1987) recognized *Pseudalopex* as a separate taxon and treated it as congeneric with *Lycalopex*, using the first name for the genus. Wozencraft (1989) placed the culpeo fox under the genus *Dusicyon*, together with the crab-eating fox, *Cerdocyon thous* Hamilton Smith, 1839, but in a later analysis (Wozencraft, 1993) assigned the culpeo to *Pseudalopex* and agreed with Berta (1987) in treating *Lycalopex* as congeneric. Zunino et al. (1995) followed Berta and Wozencraft in treating *Lycalopex* and *Pseudalopex* as congeneric but used *Lycalopex* for the genus because it has 2 years priority. Finally, in a recent cladistic study of living genera of canids, Tedford et al. (1995) concluded that *Pseudalopex* is a separate genus from *Lycalopex*.

Other vernacular names for the species are zorro colorado, zorro rojo, zorro grande, and lare (Ginsberg and Macdonald, 1990). *Culpeo* may derive from the native Chilean word *culpem*, which means madness, because the animal exposes himself constantly to being killed by hunters (Molina, 1782; Osgood, 1943).

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LITERATURE CITED

ABELLO, O. 1979. Densidad de una población de zorros colorados *Dusicyon culpaeus*, en el Parque Nacional Torres del Paine (Magallanes, Chile). Informe Corporación Nacional Forestal, 7:1–26 (not seen, cited in Ginsberg and Macdonald, 1990).

ALLEN, J. A. 1905. The Mammalia of southern Patagonia: reports of the Princeton University Expeditions to Patagonia (W. B. Scott, ed.), Princeton University Press, New Jersey, 3(I):1–210.

ALVAREZ, B. V. 1960. Presencia de *Linguatula serrata* (Froelich, 1789) en *Dusicyon culpaeus* y de formas ninfales en *O. degus* y *A. b. bennetti*. Boletín Chileno de Parasitología, 15:22.

———. 1961. Investigaciones sobre echinococcosis silvestre en Chile. Biologica, 31:89–94.

BELLATI, J. 1986. Estimación de las pérdidas por zorro colorado de corderos de 1 a 60 días de edad en el Departamento de Pilcaniyeu, R. N. Presencia, 2(12):43–44.

BELLATI, J., AND J. VON THUNGEN. 1990. Lamb predation in Patagonian ranches. Pp. 263–268, *in* Proceedings of the 14th Vertebrate Pest Conference (L. R. Davis and R. E. Marsh, eds.). University of California, Davis, 360 pp.

BERTA, A. 1981. Evolution of large canids in South America. Anais II Congresso Latino Americano de Paleontología, Porto Alegre, 2:835–845.

———. 1987. Origin, diversification, and zoogeography of the South American Canidae. Fieldiana Zoology, 39:455–471.

———. 1988. Quaternary evolution and biogeography of the large South American Canidae (Mammalia: Carnivora). University of California Publications, Geological Sciences, 132: 1–149.

BLOOD, B. D., AND J. L. LELIJVELD. 1969. Studies on sylvatic echinococcosis in southern South America. Tropenmedizin und Parasitologie, 20:475–482.

BRANCH, L. C. 1994. Seasonal patterns in long-distance vocalizations of the pampas fox. Vida Silvestre Neotropical, 3:108–111.

BURMEISTER, H. 1854. Systematische Uebersicht der Thiere Brasiliens, welche während einer Reise durch die Provinzen von Rio de Janeiro und Minas Geraës gesammelt oder beobachtet wurden von Dr. H. Burmeister. Säugethiere (Mammalia). Georg Reimer, Berlin, 342 pp.

———. 1856. Erläuterungen zur Fauna Brasiliens, enthaltend Abbildungen und ausführliche Beschreibungen neuer oder ungenügend bekannter Thier-Arten. Georg Reimer, Berlin, 115 pp.

BUSTAMANTE, R. O., J. A. SIMONETTI, AND J. E. MELLA. 1992. Are foxes legitimate and efficient seed dispersers? A field test. Acta Oecologica, 13:203–208.

CABRERA, A. 1931. On some South American canine genera. Journal of Mammalogy, 12:54–67.

———. 1932. Sinopsis de los cánidos argentinos. Revista del Centro de Ingenieros Agrónomos y Centro de Estudios de Agronomía, 145:489–501.

———. 1940. Notas sobre carnívoros sudamericanos. Notas del Museo de la Plata, Zoología, 29:1–22.

———. 1958. Catálogo de los mamíferos de América del Sur Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Zoología, 4:1–308.

CABRERA, A., AND J. YEPES. 1940. Mamíferos Sud-Americanos. Compañía Argentina de Editores, Buenos Aires, 370 pp.

CAPURRO, A. F., A. J. NOVARO, A. TRAVAINI, AND M. S. ROMERO. In press. Improved bile-acid thin-layer chromatography to identify feces of Neotropical carnivores. Journal of Wildlife Management.

CASTRO, S. A., S. I. SILVA, P. L. MESERVE, J. R. GUTIERREZ, L. C. CONTRERAS, AND F. M. JAKSIC. 1994. Frugivoría y dispersión de semillas de pimiento (*Schinus molle*) por el zorro culpeo (*Pseudalopex culpaeus*) en el Parque Nacional Fray Jorge (IV

Región, Chile). Revista Chilena de Historia Natural, 67:169–176.

CLUTTON-BROCK, J., G. B. CORBET, AND M. HILLS. 1976. A review of the family Canidae, with a classification by numerical methods. Bulletin of the British Museum (Natural History), Zoology, 29:119–199.

COHEN, J. A., AND M. W. FOX. 1976. Vocalizations in wild canids and possible effects of domestication. Behavioural Processes, 1:77–92.

CORLEY, J. C., G. F. FERNANDEZ, A. F. CAPURRO, A. J. NOVARO, M. C. FUNES, AND A. TRAVAINI. 1995. Selection of cricetine prey by the culpeo fox in Patagonia: a differential prey vulnerability hypothesis. Mammalia, 59:315–325.

CRESPO, J. A. 1975. Ecology of the pampas gray fox and the large fox (culpeo). Pp. 179–191, *in* The wild canids (M. W. Fox, ed.). Van Nostrand Reinhold Company, New York, 508 pp.

CRESPO, J. A., AND J. DE CARLO. 1963. Estudio ecológico de una población de zorros colorados. Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Ecología, 1: 1–55.

DIUK WASSER, M. A. 1995. Selección de hábitat del zorro colorado (*Pseudalopex culpaeus*) en la Patagonia argentina. Licenciate thesis, Universidad de Buenos Aires, Argentina, 61 pp.

DURÁN, J. C., P. E. CATTAN, AND J. L. YAÑEZ. 1987. Food habits of foxes (*Canis* sp.) in the Chilean National Chinchilla Reserve. Journal of Mammalogy, 68:179–181.

EBENSPERGER, L. A., J. E. MELLA, AND J. A. SIMONETTI. 1991. Trophic-niche relationships among *Galictis cuja*, *Dusicyon culpaeus*, and *Tyto alba* in central Chile. Journal of Mammalogy, 72:820–823.

EISENBERG, J. E. In press. Mammals of the Neotropics. Vol. 3. University of Chicago Press, Chicago.

EWER, R. F. 1973. The Carnivores. Cornell University Press, New York, 494 pp.

FISCHER, G. 1814. Zoognosia tabulis synopticis illustrata. Quadrupedum reliquorum, cetorum et monotrymatum descriptionem continens. Typis Nicolai Sergeidis Vsevolozky, Moscow, 3:1–605.

FUENTES, E. R., AND F. M. JAKSIC. 1979. Latitudinal size variation of Chilean foxes: tests of alternative hypotheses. Ecology, 60: 43–47.

GINSBERG, J. R., AND D. W. MACDONALD. 1990. Foxes, wolves, jackals, and dogs. An action plan for the conservation of canids. International Union for the Conservation of Nature and Natural Resources, Gland, Switzerland, 116 pp.

GITTLEMAN, J. L. 1986. Carnivore brain size, behavioral ecology, and phylogeny. Journal of Mammalogy, 67:23–36.

GRAY, J. E. 1837*a*. Report to the Zoological Society. Proceedings of the Zoological Society of London, 1836:87–88.

———. 1837*b*. Descriptions of some new or little known Mammalia, principally in the British Museum Collection. The Magazine of Natural History, and Journal of Zoology, Botany, Mineralogy, Geology, and Meteorology, 1:577–587.

———. 1843. List of the specimens of Mammalia in the collection of the British Museum. British Museum (Natural History), London, 216 pp.

GRIGERA, D. E., AND E. H. RAPOPORT. 1983. Status and distribution of the European hare in South America. Journal of Mammalogy, 64:163–166.

GRIMWOOD, I. 1969. Notes on the distribution and status of some Peruvian mammals. American Committee for International Wildlife Protection and the New York Zoological Society, Special Publication 21:1–186 (not seen, cited in Ginsberg and Macdonald, 1990).

HAMILTON SMITH, C. 1839. The natural history of dogs. Vol. I. The naturalist's library (W. Jardine, ed.). W. H. Lizars, Edinburgh, 9:1–267.

HILZHEIMER, M. 1906. *Papio mundamensis*, *Felis deliensis*, *Canis reissii* und andre neue Sägethiere. Zoologischer Anzeiger, 30:109–118.

HOPKINS, G. H. E. 1949. The host-associations of the lice of mammals. Proceedings of the Zoological Society of London, 119: 387–604.

HOUSSE, R. 1953. Animales salvajes de Chile. Ediciones Universidad de Chile, Santiago, 189 pp (not seen, cited in Medel and Jaksic, 1988).

HUBER, A. 1925. El zorro y su piel en la República Argentina. República Argentina, Ministerio de Agricultura, Sección Propaganda e Informes, 360:1–11.

IRIARTE, J. A., AND F. M. JAKSIC. 1986. The fur trade in Chile: an overview of seventy-five years of export data (1910-1984). Biological Conservation, 38:243–253.

IRIARTE, J. A., J. E. JIMÉNEZ, L. C. CONTRERAS, AND F. M. JAKSIC. 1989. Small-mammal availability and consumption by the fox, *Dusicyon culpaeus*, in central Chilean scrublands. Journal of Mammalogy, 70:641–645.

IUCN. 1988. Significant trade in wildlife: a review of selected species in CITES Appendix II: mammals. International Union for the Conservation of Nature and Natural Resources, Gland, Switzerland, 1:1–80.

JAKSIC, F. M. 1986. Predation upon small mammals in shrublands and grasslands of southern South America: ecological correlates and presumable consequences. Revista Chilena de Historia Natural, 59:209–221.

———. 1989. What do carnivorous predators cue in on: size or abundance of mammalian prey? A crucial test in California, Chile, and Spain. Revista Chilena de Historia Natural, 62: 237–249.

JAKSIC, F. M., AND J. A. SIMONETTI. 1987. Predator/prey relationships among terrestrial vertebrates: an exhaustive review of studies conducted in southern South America. Revista Chilena de Historia Natural, 60:221–244.

JAKSIC, F. M., AND J. L. YÁÑEZ. 1980. Quien controla las poblaciones de conejos introducidos. Medio Ambiente (Chile), 4:41–44.

———. 1983. Rabbit and fox introduction in Tierra del Fuego. History and assessment of the attempts of biological control of rabbit infestation. Biological Conservation, 26:367–374.

JAKSIC, F. M., P. FEINSINGER, AND J. E. JIMÉNEZ. 1996. Ecological redundancy and long-term dynamics of vertebrate predators in semiarid Chile. Conservation Biology, 10:252–262.

JAKSIC, F. M., H. W. GREENE, AND J. L. YÁÑEZ. 1981. The guild structure of a community of predatory vertebrates in central Chile. Oecologia (Berlin), 49:21–28.

JAKSIC, F. M., P. SCHLATTER, AND J. L. YÁÑEZ. 1980. Feeding ecology of central Chilean foxes, *Dusicyon culpaeus* and *Dusicyon griseus*. Journal of Mammalogy, 61:254–260.

JAKSIC, F. M., J. L. YÁÑEZ, AND J. R. RAU. 1983. Trophic relations of the southernmost populations of *Dusicyon* in Chile. Journal of Mammalogy, 64:693–697.

JAKSIC, F. M., J. E. JIMÉNEZ, S. A. CASTRO, AND P. FEINSINGER. 1992. Numerical and functional response of predators to a long-term decline in mammalian prey at a semi-arid Neotropical site. Oecologia, 89:90–101.

JAKSIC, F. M., P. L. MESERVE, J. R. GUTIERREZ, AND E. L. TABILO. 1993. The components of predation on small mammals in semiarid Chile: preliminary results. Revista Chilena de Historia Natural, 66:305–321.

JIMÉNEZ, J. E. 1993. Comparative ecology of *Dusicyon* foxes at the Chinchilla National Reserve in northcentral Chile. M.S. thesis, University of Florida, Gainesville, 168 pp.

JIMÉNEZ, J. E., J. L. YÁÑEZ, AND F. M. JAKSIC. 1996. Inability of thin-layer chromatography to distinguish feces from congeneric foxes by their bile acid contents. Acta Theriologica, 41: 211–215.

JIMÉNEZ, J. E., J. L. YÁÑEZ, E. L. TABILO, AND F. M. JAKSIC. 1995. Body size of Chilean foxes: a new pattern in light of new data. Acta Theriologica, 40:321–326.

JOHNSON, W. E., AND W. L. FRANKLIN. 1994*a*. Role of body size in the diets of sympatric gray and culpeo foxes. Journal of Mammalogy, 75:163–174.

———. 1994*b*. Conservation implications of South American grey fox (*Dusicyon griseus*) socioecology in the Patagonia of southern Chile. Vida Silvestre Neotropical, 3:16–23.

———. 1994*c*. Spatial resource partitioning by sympatric grey fox (*Dusicyon griseus*) and culpeo fox (*Dusicyon culpaeus*) in southern Chile. Canadian Journal of Zoology, 72:1788–1793.

JOHNSON, W. E., W. L. FRANKLIN, AND J. A. IRIARTE. 1992. The mammalian fauna of the Northern Chilean Patagonia: a biogeographical dilemma. Mammalia, 56:446–457.

JOHNSON, W. E. 1992. Comparative ecology of two sympatric South American foxes, *Dusicyon griseus* and *D. culpaeus*. Ph.D. dissertation, Iowa State University, Ames, 142 pp.

KRAGLIEVICH, J. L. 1952. Un cánido del Eocuaternario de Mar del Plata y sus relaciones con otras formas brasileñas y norteamericanas. Revista del Museo Municipal de Ciencias Naturales y Tradicional de Mar del Plata, Buenos Aires, Argentina, 1:53–70.

KRAGLIEVICH, L. 1930. Craneometría y clasificación de los cánidos sudamericanos, especialmente los argentinos actuales y fósiles. Physis, 10:35–73.

LANGGUTH, A. 1967. Sobre la identidad de *Dusicyon culpaeolus* (Thomas) y de *Dusicyon inca* (Thomas). Neotropica, 13:21–28.

———. 1969. Die sudamerikanischen Canidae unter besonderer ¡Berucksichtigung des Mahnenwolfes *Chrysocyon brachyurus* Illiger. Zeitschrift für wissenschaftliche Zoologie, 179:1–188.

———. 1970. Una nueva clasificacion de los canidos sudamericanos. Actas IV Congreso Latinoamericano de Zoologia, 1:129–143.

———. 1975. Ecology and evolution in the South American canids. Pp. 192–206, *in* The wild canids (M. W. Fox, ed.). Van Nostrand Reinhold Company, New York, 508 pp.

LEÓN-LOBOS, P. M., AND M. T. KALIN-ARROYO. 1994. Germinación de semillas de *Lithrea caustica* (Mol.) H. et A. (Anacardiaceae) dispersadas por *Pseudalopex* spp. (Canidae) en el bosque esclerófilo de Chile central. Revista Chilena de Historia Natural, 67:59–64.

MARES, M. A., R. A. OJEDA, AND M. P. KOSCO. 1981. Observations on the distribution and ecology of the mammals of Salta Province, Argentina. Annals of the Carnegie Museum, 50: 151–206.

MARQUET, P. A., L. C. CONTRERAS, J. C. TORRES-MURA, S. I. SILVA, AND F. M. JAKSIC. 1993. Food habits of *Pseudalopex* foxes in the Atacama desert, pre-Andean ranges, and the high-Andean plateau of northernmost Chile. Mammalia, 57:130–135.

MARTÍNEZ, D. R., J. R. RAU, AND F. M. JAKSIC. 1993. Respuesta numérica y selectividad dietaria de zorros (*Pseudalopex* spp.) ante una reducción de sus presas en el norte de Chile. Revista Chilena de Historia Natural, 66:195–202.

MEDEL, R. G., AND F. M. JAKSIC. 1988. Ecología de los cánidos sudamericanos: una revisión. Revista Chilena de Historia Natural, 61:67–79.

MESERVE, P. L. 1988. Are predator diets a consequence of human disturbance in central Chile?—a reply to Simonetti. Revista Chilena de Historia Natural, 61:159–161.

MESERVE, P. L., E. J. SHADRICK, AND D. A. KELT. 1987. Diets and selectivity of two Chilean predators in the northern semiarid zone. Revista Chilena de Historia Natural, 60:93–99.

MESERVE, P. L., J. R. GUTIÉRREZ, J. A. YUNGER, L. C. CONTRERAS, AND F. M. JAKSIC. 1996. Role of biotic interactions in a small mammal assemblage in semiarid Chile. Ecology, 77:133–148.

MOLINA, G. I. 1782. Saggio sulla storia naturale del Chili. Stamperia di Santo Tommaso d'Aquino, Bologna, Italy, 368 pp.

MORENO, P. I., C. VILLAGRAN, P. A. MARQUET, AND L. G. MARSHALL. 1994. Quaternary paleobiogeography of northern and central Chile. Revista Chilena de Historia Natural, 67:487–502.

NOVARO, A. J. 1991. Feeding ecology and abundance of a harvested population of culpeo fox (*Dusicyon culpaeus*) in Patagonia. M. S. thesis, University of Florida, Gainesville, 103 pp.

———. 1993. Culpeo foxes in Patagonia. Canid News, 1:15–17.

———. 1995. Sustainability of harvest of culpeo foxes in Patagonia. Oryx, 29:18–22.

NOVARO, A. J., AND M. C. FUNES. 1994. Impact of hunting on Argentinean foxes. Canid News, 2:19–20.

OSGOOD, W. H. 1934. The genera and subgenera of South American Canidae. Journal of Mammalogy, 15:45–50.

———. 1943. The mammals of Chile. Field Museum of Natural History, Zoological Series, 30:1–268.

PASCUAL, R. 1966. Paleontografía bonaerense: Fascículo IV: Vertebrata. Comisión de Investigación Científica de Buenos Aires, La Plata, Argentina, 202 pp.

PHILIPPI, R. A. 1896. Dos animales nuevos de la fauna Chilena. Anales de la Universidad de Santiago de Chile, 94:541–546.

———. 1903. Einige neue Chilenische Canis-Arten. Archiv für Naturgeschichte, 69:155–160.

PRICHARD, H. H. 1902. Through the heart of Patagonia. D. Appleton and Company, New York, 346 pp.

RAU, J. R., M. DELIBES, AND J. F. BELTRAN. 1987. Estudio comparado de la dieta de los zorros mediterráneos (Carnivora, Canidae). Anales del Museo de Historia Natural de Valparaíso, 18:163–168.

REDFORD, K. H., AND J. F. EISENBERG. 1992. Mammals of the Neotropics: the southern cone. University of Chicago Press, Chicago, 2:1–420 pp.

SCHANTZ, P. M., R. D. LORD, AND O. DE ZAVALETA. 1972. *Echinococcus* in the South American red fox (*Dusicyon culpaeus*) and the European hare (*Lepus europaeus*) in the Prov. of Neuquén, Argentina. Annals of Tropical Medicine and Parasitology, 66:479–485.

SCHANTZ, P. M., C. COLLI, A. CRUZ-REYES, AND U. PREZIOSO. 1976. Sylvatic echinococcosis in Argentina. II. Susceptibility of wild carnivores to *Echinococcus granulosus* (Batsch, 1786) and host-induced morphological variation. Tropenmedizin und Parasitologie, 27:70–78.

SCHANTZ, P. M., A. CRUZ-REYES, C. COLLI, AND R. D. LORD. 1975. Sylvatic echinococcosis in Argentina. I. On the morphology and biology of strobilar *Echinococcus granulosus* (Batsch, 1786) from domestic and sylvatic animal hosts. Tropenmedizin und Parasitologie, 26:334–344.

SIMONETTI, J. A. 1986. Human-induced dietary shift in *Dusicyon culpaeus*. Mammalia, 50:406–408.

———. 1988. The carnivorous predatory guild of central Chile: a human-induced community trait? Revista Chilena de Historia Natural, 61:23–25.

STEIN, M., D. M. SURIANO, AND A. J. NOVARO. 1994. Nematodes parásitos de *Dusicyon griseus*, *D. culpaeus* y *Conepatus chinga* (Mamifera: Carnivora) en Neuquén, Argentina. Sistemática y ecología. Boletín Chileno de Parasitología, 49:60–65.

SZIDAT, L. 1960. *Echinococcus patagonicus* sp.nov. (Cestoda), parásito del zorro *Dusicyon culpaeus culpaeus* (Mol.). Neotropica, 6:13–16.

———. 1963. Studien über den Erreger der alveolaren Echinococcenkrankheit des Menschen in Sudamerika. Zeitschrift für Parasitenkunde, 23:80–91.

TEDFORD, R. H., B. E. TAYLOR, AND X. WANG. 1995. Phylogeny of the Caninae (Carnivora: Canidae): the living taxa. American Museum Novitates, 3146:1–37.

THOMAS, O. 1914*a*. On various South-American mammals. Annals and Magazine of Natural History, Series 8, 13:345–363.

———. 1914*b*. Three new S.-American mammals. Annals and Magazine of Natural History, Series 8, 13:573–575.

TROUESSART, E. L. 1904. Catalogus mammalium tam viventium quam fossilium. Quinquennale supplementium, 929 pp.

———. 1906. Sur une espece nouvelle du genre *Icticyon* (*Speothos*), provenant de l'Equateur. Comptes Rendus de l'Académie des Sciences, Paris, 143:1184–1186.

VAN GELDER, R. G. 1978. A review of canid classification. American Museum Novitates, 2646:1–10.

VITULLO, A. D., AND G. A. ZULETA. 1992. Cytogenetics and fossil record: confluent evidence for speciation without chromosomal change in South American canids. Zeitshrift für Säugetierkunde, 57:248–250.

VOIPIO, P. 1950. Evolution at the population level with special reference to game animals and practical game management. Papers on Game Research (Helsinki), 5:1–176.

VON THUNGEN, J. 1991. Utilidad de las estaciones de cebado. I. Determinación de la densidad poblacional de zorros. Pp. 10–13, *in* Actas de la III Reunión Patagónica de Manejo de Poblaciones de Zorros (M. C. Funes and A. J. Novaro, eds.). Imprenta Universitaria, Neuquén, Argentina, 53 pp.

WAYNE, R. K., AND S. J. O'BRIEN. 1987. Allozyme divergence within the Canidae. Systematic Zoology, 36:339–355.

WAYNE, R. K., B. VAN VALKENBURGH, P. W. KAT, T. K. FULLER, W. E. JOHNSON, AND S. J. O'BRIEN. 1989. Genetic and morphological divergence among sympatric canids. Journal of Heredity, 80:447–454.

WEBB, S. D. 1985. Late Cenozoic mammal dispersals between the Americas. Pp. 357–386, *in* The great American biotic interchange (F. G. Stehli and S. D. Webb, eds.). Plenum Press, New York, 532 pp.

WING, E. S. 1989. Human use of canids in the central Andes. Pp. 265–278, *in* Advances in Neotropical mammalogy (K. H. Redford and J. F. Eisenberg, eds.). The Sandhill Crane Press, Gainesville, 614 pp.

WOZENCRAFT, W. C. 1989. Classification of the recent Carnivora. Pp. 569–593, *in* Carnivore behavior, ecology, and evolution (J. L. Gittleman, ed.). Cornell University Press, Ithaca, New York, 620 pp.

———. 1993. Order Carnivora. Pp. 279–348 *in* Mammal species of the world: a taxonomic and geographic reference. Second ed. (D. E. Wilson and D. M. Reeder, eds.). Smithsonian Institution Press, Washington, D.C., 1206 pp.

YAHNKE, C. J., ET AL. 1996. Darwin's fox: a distinct endangered species in a vanishing habitat. Conservation Biology, 10:366–375.

YAÑEZ, J., AND F. JAKSIC. 1978. Rol ecológico de los zorros (*Dusicyon*) en Chile central. Anales del Museo de Historia Natural de Valparaíso, 11:105–112.

YAÑEZ, J., AND J. RAU. 1980. Dieta estacional de *Dusicyon culpaeus* (Canidae) en Magallanes. Anales del Museo de Historia Natural de Valparaíso, 13:189–191.

ZUNINO, G. E., O. B. VACCARO, M. CANEVARI, AND A. L. GARDNER. 1995. Taxonomy of the genus *Lycalopex* (Carnivora: Canidae) in Argentina. Proceedings of the Biological Society of Washington, 108:729–747.

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A. J. NOVARO, DEPARTMENT OF WILDLIFE ECOLOGY AND CONSERVATION, 303 NEWINS ZIEGLER HALL, UNIVERSITY OF FLORIDA, GAINESVILLE, FL 32611; PRESENT ADDRESS, PUEYRREDON 1505 PISO 3, 1118 BUENOS AIRES, ARGENTINA.